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STUDIES OF THE DEVELOPMENT OF THE PIPERACEAE

II. THE STRUCTURE AND SEED-DEVELOPMENT OF *PEPEROMIA* *HISPIDULA*¹

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The following study is concerned with *Peperomia hispidula* A. Dietr. This species, which has one of the most peculiar types of embryo sac thus far discovered among angiosperms (Johnson 1907), also has a surprisingly simple vegetative structure, as will be briefly shown here. The whole development of the flower, embryo sac and seed of this *Peperomia* will be described in some detail in order that the development of other species, to be described later, may be compared with it and thus the variety of development found within the genus made evident.

The material used in this investigation was gathered near the Tropical Station of the New York Botanical Garden, at Cinchona, Jamaica, during visits made to that island in 1903, 1906, and 1910. These visits were made possible by grants from the Botanical Society of America, from the Bache Fund, and from the Carnegie Institution of Washington. It is a pleasure to acknowledge here the aid received from these sources and also the courtesies extended by the New York Botanical Garden, in the use of its Cinchona Station, and by the Department of Agriculture of Jamaica. M. Cassimir deCandolle is here thanked for determining the species of this and other *Peperomias* for the author.

The flowers, fruits and vegetative structures of the plant were carefully fixed by the writer, in several mixtures of chromic and acetic acids, in Flemming's fluid, and, in the case of some older seeds, in a mixture of acetic acid and alcohol. The study of the preserved material has been carried on at the Johns Hopkins University and at the Harpswell Laboratory.

We will, for the sake of clearness, arrange the presentation of the features to be discussed under the following heads: *A.* Habit and vegetative structure. *B.* Development of the spike and flower.

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C. The stamen, microspore and pollen tube. D. The carpel, fruit, ovule and seed. E. The megaspore, embryo sac, embryo and endosperm. F. Germination. G. Conclusion.

A. HABIT AND VEGETATIVE STRUCTURE

Peperomia hispidula A. Dietr. is a small and very delicate *Peperomia* found (according to deCandolle, Dahlstedt et al.) in Jamaica, Costa Rica, Colombia, Ecuador, Brazil and Argentina. It occurs in damp mountain forests. In Jamaica it is found on the ridge and north side of the Blue Mountains, from 1,600 meters upward. It grows among the mosses and ferns, usually in dense shade, on the nearly saturated humus of the forest floor.

The mature plant is small and decumbent, with the terminal 5 or 6 internodes of each branch assurgent (Swartz 1794, pl. IV). It may flower when only 4 or 5 centimeters long, and the largest plants seen were rarely more than 10 centimeters in length. The stem is delicate, usually whitish or nearly transparent, though, if growing in the light, it is sometimes decidedly greenish. It is sparsely branched, and cylindrical, except for the two ridges extending down each internode downward from the margins of the slightly winged petiole (fig. 10). The internodes are from 30 to 40 millimeters long, and 1 to $1\frac{1}{2}$ millimeters in diameter. At each internode are some 15 to 25 multicellular bristles, similar to those of the leaf blade to be mentioned below. These stiff, tapering bristles consist of 8 to 12 highly vacuolated, thick-walled cells in one longitudinal series, are often a millimeter long and have a diameter of $40\ \mu$ (figs. 1, 2). These trichomes stand out in all directions at the node and just above and below it. The stem roots freely by groups of 10 or 12 roots formed near the nodes, and more rarely by scattered roots along the internodes. These roots are only .2 or .3 millimeter in diameter, are but 20 or 30 millimeters long, and are sparsely branched.

The delicate, short petioled, alternately arranged leaves are nearly orbicular, though often somewhat cordate at the base. The larger ones may be 8 or 10 millimeters in diameter and have petioles 3 or 4 millimeters long. The petiole is slightly margined at the sides, and these two wings end against the dorsal side of the lamina just above its base (figs. 1, 14). The two basal lobes of the lamina are connected with each other by a ridge extending across the anterior face of the petiole where it joins the lamina (fig. 1). The insertion of the

blade thus approaches the peltate type. Over the upper surface of the lamina, chiefly near the edges, are scattered some 10 to 25 bristle-like hairs of 10 to 20 cells each, and of about one millimeter in length (figs. 1, 3). The whole leaf has almost the aspect of that of a large hydrophytic bryophyte. As the hairs mentioned are not easily wetted it seems possible that these and the hairs at the base of the petiole may serve to prevent the adherence of water to the surface of this denizen of very damp habitats. It is also possible that these hairs may serve as an obstruction to small insects creeping over the plant.

The internal structure of the vegetative organs is also relatively very simple. The delicate, sparsely branched roots have a small, thin root-cap (fig. 4). The youngest root hairs are found about two or three diameters of the root behind the apex of the latter. These hairs may reach a diameter of 10 or 12 μ and a length of a millimeter or more (fig. 6). Fungus hyphae enter the root from without and push among and into the cortical cells. These hyphae are little branched, thick-walled, non-septate and from 4 to 5 μ in thickness. Coiled tangles of these fungus threads with beadlike swellings are found in the layer of the cortex just outside the endodermis (figs. 5, 6, 7). In some places the hyphae become greatly swollen to form sac-like expansions that may become 15 μ in diameter and 54 μ long (fig. 8). Whether these hyphae have the function, as well as the appearance, of an endophytic mycorrhiza cannot yet be stated with certainty.

The oldest roots seen still had some root hairs on them; the epidermis was intact and the outer walls of its cells were but slightly thickened or cutinized. The cells of the epidermis are 20 or 25 μ in radial and tangential thickness and 50 or 60 μ long (figs. 5, 6). The cortex of the mature root is of 5 or 6 layers of cells, which are 12 to 40 μ in diameter and 100 to 150 μ long. There are numerous intercellular spaces between the cells of the inner layers of the cortex. Many of these are occupied by the fungous hyphae mentioned above (fig. 6). The radial walls of the endodermis are but slightly thickened but are markedly crinkled, as may be seen in a tangential section (figs. 5, 9). These cells are 12 to 20 μ in diameter and 150 μ long.

The whole central cylinder of the mature root is only 90 or 100 μ in diameter and consists of but 40 or 50 cells in cross section (fig. 6). Of these cells two or three are differentiated as water-conducting elements. One, at the center of the stele, is a vessel 12 or 15 μ in diameter and with ring-like and spiral thickenings on its walls. A

smaller, ringed duct 7 or 8 μ thick, lies on each side of this (figs. 5, 6). On each side of the plane in which these three ducts lie is seen a small group of phloem elements, apparently containing only one or two sieve tubes each (fig. 6). The whole thus makes up a very simple diarch bundle. The other elements of the stele are thin-walled cells, about 8 or 10 μ in diameter and 100 to 140 μ long. There is no evidence in the oldest roots seen of the formation of any cambium zone, nor even of the development of any secondary xylem or phloem in the bundles (figs. 5, 6). It is evident that in this creeping plant new water-absorbing and water-conducting tissue is added, not by the development of secondary tissue in roots already present but by the formation of entirely new roots on younger portions of the plant. The time of persistence of the roots was not determined.

The internodes of the delicate, sparingly branched stem are also extremely simple in internal structure. The epidermis, as seen in transverse section is made up of a single layer of cells which are about 15–30 μ wide and thick and 40–100 μ long. Interspersed with these are occasional rather cubical oil cells, and the similarly shaped cells which bear, or have borne, the two-celled, knobbed hydathodes (figs. 10, 12, 13). The latter are identical in structure with those shown in various stages of development in the figures of flower and fruit. The outer walls of the ordinary epidermal cells are but slightly cutinized, but this thin cuticle is peculiar in being thrown into numerous minute corrugations (fig. 13). The middle, cuticular layer of the outer cell wall, often 2 μ thick, is much thicker than the outer cutin layer, while the inner cellulose layer has only twice the thickness of the cutin. The outer walls of the oil cells are very similar in thickness and structure to those of the epidermal cells, while the outer walls of the hydathodes are very thin and without distinguishable layers.

The cortex of the mature internode consists, in addition to the epidermis, of four or five layers of thin-walled cells which vary from 30 to 200 μ in diameter and from 150 to 250 μ in length. Small air-spaces are present, especially between the cells of the outer layers. The endodermis consists of but 18 or 20 cells in transverse section. These have a diameter of from 20 to 60 μ and a length of 50 to 70 μ (figs. 10, 11). The radial walls are but slightly thickened, and the crinkling is coarser than that noted in the endodermis of the root. The whole central cylinder of an internode, within the endodermis, is 150 to 250 μ across, and is often flattened in the plane of the leaf next

below (figs. 10, 11). The transverse section of the stele consists of only about 150 cells, which vary in diameter from 5 to 25 μ and in length from 20 to 100 μ . There are usually two distinct groups of primary xylem, one near each edge of the flattened bundle (fig. 11). Each group contains from 4 to as many as 8 or 10 ducts which are ringed, or less often spirally thickened. These ducts vary from 10 to 30 μ in diameter and are often 500 μ in length. Between, and arranged around these ducts are thin-walled parenchymatous cells, which may become 75 μ long. A group of 20 to 30 phloem cells is found outside each group of xylem and on the same radius (fig. 11). Each of the phloem groups consists of 6 to 8 sieve tubes, and of rather more numerous cambiform cells with surrounding parenchyma.

In the stem, as in the root, no indication was found of the formation of a cambium ring nor even of any formation of secondary xylem or phloem. The small amount of water-conducting tissue formed in the root and stem of this *Peperomia* is a fact evidently related to its moist habitat. So small a plant, creeping close to the soil, and growing in a very humid air, must lose very little water by transpiration and thus needs to carry but little water in its conducting system. Moreover, that little water needs to be carried but a short distance, because new groups of roots are formed frequently along the stem as it grows, so that every internode or pair of internodes, except those near the apex, has its own direct connection with the water supply in the soil.

As contrasted with the type of conducting system just described we find that the stem of xerophytic species of *Peperomia*, such as *P. reflexa* or *P. verticillata*, have much more highly developed bundles. In the latter, for example, there are 10 or 12 bundles in two concentric rings. Even in the rather delicate, creeping *P. filiformis*, growing in the same damp forests with *P. hispidula*, there is a ring of four bundles in the stele.

The internal structure of the leaf of *Peperomia hispidula* is also simpler than that of any other species of the genus known to the writer.

The petiole, as seen in cross section (fig. 14), is somewhat flattened dorsiventrally and has a slight wing at each edge. The epidermis consists of rather irregular cells with slightly thickened outer walls, interspersed with scattered oil-cells and hydathodes. The wings of the petiole are made up solely of two layers of the epidermis, or, in some portions, of these and a third layer pushed between them (fig. 14). At

the top and toward the base of the petiole are found the simple or branched, bristle-like trichomes (figs. 1, 2). There are three, nearly equal, vascular bundles in the petiole, one median and two marginal. Of the latter, one arises on that side of the xylem strand which is on the side of the stem opposite the leaf. The other marginal bundle, together with the median bundle of the petiole and the bundle from the axillary branch, arises from the other xylem strand of the stele. Each bundle of the petiole consists of 40 or 50 cells in cross section, and includes 5 or 6 thickened ducts and a similar number of phloem elements. These bundles are surrounded, in the cross section, by about 100 parenchymatous cells, 25 to 60 μ in diameter and 40 to 70 μ long, between which are numerous, small air-canals (figs. 14, 15).

The blade of the leaf has a pinnately arranged, sparingly branched vascular system, that supports a delicate but bristly lamina of but 3 or 4 cells in thickness (figs. 1, 2, 17). The epidermis of the upper surface consists of irregularly polygonal cells 40 to 60 μ across, from among which arise the ten- or fifteen-celled, bristle-like trichomes (fig. 3). Each trichome rests upon a ring of 5 or 6 surface cells, that is raised slightly above the upper surface of the leaf and is free from the underlying palisade layer. Stomata are wanting from the upper side of the leaf. Oil-cells are about as abundant as on the lower side. Hydathodes are rather less abundant than below. The epidermis of the lower side consists chiefly of wavy-margined cells, often 100 μ long, sparsely interspersed with stomata, oil-cells and hydathodes (fig. 18). The epidermal cells of the margin and of the lower surface of the veins are much elongated, and have oil-cells only scattered among them, except at the glandular tip of the leaf, where hydathodes may occur also (fig. 18). The cutin layer of the epidermal cells is often striate like that of the stem, especially in cells at the edge of the leaf. The average number of stomata in the areas between the veins is about 40 per square millimeter (fig. 18). The form of the guard cells as seen from the surface is of a type rather common among angiosperms (fig. 19). When viewed in cross section the guard cells are seen to be peculiar in having a thin, sharp-edged cutin lip bordering the stoma, much like that shown by Haberlandt ('87, and '09, p. 424, 427) to be characteristic of aquatics or land plants of very moist habitats, such as *Lemna*, *Trianea*, *Fegatella*, etc. (fig. 20). Moreover, this lip is so broad, and the ventral walls of the guard cells next the slit so widely separated in all sections seen, that it seems likely that

these stomata are also like those mentioned in being unable to close at all completely. It seems evident that such a stoma would be no serious disadvantage to a plant of very humid habitats. It is possible that Haberlandt's suggestion, that the sharp-edged guard cells of the plants mentioned prevent closing of the stomata by water drops, may also be applicable to this *Peperomia*. The only portions of the lower side of the leaf where stomata are more abundant than is indicated above are the areas underlying the glandular swellings of the veins near the margin of the leaf (G, in fig. 1). Here the stomata become relatively numerous, though apparently not differing in size or structure from the stomata occurring on the thinner portions of the lamina (figs. 17, 18, 21). It is probable that these stomata serve as water stomata, as we shall see later, when speaking of the glands with which they are associated.

The mesophyll portion of the lamina, between the veins, consists of a single layer of slightly specialized, nearly isodimensional palisade cells, and of one or, near the veins, of two layers of sponge parenchyma (figs. 16, 17). Near the margin of the lamina the tissue between the upper and lower epidermis may consist solely in addition to the single layer of palisade, of one layer of very scattered parenchyma cells (figs. 17, 21). The palisade cells are 40 to 45 μ in vertical length and vary from 20 to 45 μ in diameter. Each contains a single large nucleus and from 15 to 25 chromatophores. These cells are closely in contact with other cells except at their rounded inner ends, which are surrounded by considerable air-spaces and rest upon one or more of the underlying parenchyma cells. The latter are often 10 to 15 μ thick and 40 or 50 μ long tangentially, and may contain 12 or 15 chromatophores, which are, however, only about half as bulky as the chromatophores of the palisade cells. It is evident, from their contents and from their relation to other tissues, that these sponge-parenchyma cells must serve not only for photosynthesis but likewise for the conduction of the products of this process from the palisade cells to the vascular bundles. They must evidently also carry water in the reverse direction. The water-storing hypodermis, characteristic of the leaves of all other *Peperomias* studied except those of *P. pellucida* and *P. tenera* (Jäderholm, 1898) is entirely wanting in the leaf of *P. hispidula*. Moreover, there is no evidence from the structure of the epidermis, that this latter tissue serves for water-storage in our species, as Jäderholm says it does in *P. pellucida*. In the leaf of *P. hispidula* then it is evident that we

have the mesophyll structure of the aerial, dicotyledonous leaf reduced to about its simplest possible terms.

The vascular system of the lamina of *Peperomia hispidula* is derived from the three vascular bundles of the petiole, which enter the blade separately. The medium bundle forms the midrib, which gives rise from its upper half to two pairs of lateral veins (fig. 1). Each of the two lateral bundles from the petiole forks soon after entering the blade, and the two divisions so formed are connected with each other and with the branches from the midrib in the manner shown in figure 1. The submarginal vein arising from these fusions contains, for most of its length, only three or four vascular elements, and the leaf is but slightly increased in thickness in this region (fig. 17). Each of the three veins entering the base of the blade contains, on the contrary, several times this amount of vascular tissue, and each, with the tissue about it, forms a rib two or three times the thickness of the rest of the lamina. The tissue of these ribs, outside the vascular strands, consists generally of slightly modified parenchyma, surrounded by an epidermis with a few oil cells scattered through it (fig. 16). At the end of the midrib, however, and at one other point on each lateral margin of the blade, there is a broader, more massive thickening of the tissue about the veins. At these points the thickening projects chiefly on the upper side of the lamina (figs. 1, 18, 21). These swellings may be 10 or 11 cells thick, and consist of rounded parenchymatous cells surrounded by intercellular spaces connecting quite directly with those immediately below the numerous stomata (figs. 18, 21). The latter are grouped, without regularity of orientation, over the whole of this glandular swelling (fig. 21). The rounded cells of the swelling have few chloroplasts, large vacuoles and rather large nuclei. The whole structure of the thickenings is closely similar to that described for the water-secreting glands of *Tropaeolum*. Unfortunately the plants brought to Baltimore for the study of these structures in the living *Peperomia* did not live, and I therefore have no experimental evidence concerning the function of these swellings.

Considering the structure of the leaf as a whole, with its non-wettable bristles, its delicate texture, thin cuticle, limited vascular supply, and its well-developed glands evidently fitted for water secretion, it is clear that we have in this *Peperomia* a pretty highly specialized plant. This leaf structure, together with the type of root structure and stem structure noted above, make this species well fitted for the dense, reeking forest which it inhabits.

It is evident from a comparison of this *Peperomia* with the several types in the series of Brazilian species studied by Jäderholm, that *P. hispidula* is a species diverging farthest from the vegetative structure most characteristic of the genus as a whole. The gross and minute structure of the root, stem and leaf of *P. hispidula* are far simpler than those of most species, and are even somewhat simpler than in *P. delictula* and *P. tenera*, the simplest types thus far described (Jäderholm, 1898). It seems altogether possible that the highly peculiar type of embryo-sac development found in *P. hispidula* is to be attributed in some way to the same environmental conditions in its habitat that seem to have modified its vegetative structure so profoundly.

B. THE DEVELOPMENT OF SPIKE AND FLOWER

The flowers of *Peperomia hispidula* are arranged in terminal spikes, which may occur in series, one spike opposite each of the four or five terminal leaves of the shoot (figs. 1, 22, 23). The spike consists of from 6 to 14 flowers (commonly there are 9 or 10). When the spike is mature it may, with its stalk, have a length of 15 millimeters (fig. 22). The axis of the mature spike is about half a millimeter in diameter, and the flowers are widely scattered along it. The vascular system of the spike is of a single central bundle, similar to that of the stem (figs. 23, 35). The vascular bundle of each flower runs down through one internode below the insertion of the bract before joining that of the axis (fig. 56).

Each flower consists of a single ovary and two rather long-stalked stamens, all borne in the axil of a short-stalked bract with an orbicular end about half a millimeter in diameter (figs. 22, 25). The lowest bract of the spike generally bears the usual carpel and two stamens above it, but at the tip of the spike are found from one to four or five bract-like outgrowths of the axis, which are entirely without rudiments of either pistil or stamens (fig. 22). Only in rare cases were unisexual flowers found, and these were always pistillate only. The distribution of sexes is therefore much more definite and constant here than in *Piper Betel* (Johnson, 1910, p. 716). The pistils and stamens initiated, however, often fail to produce mature embryo sacs and microspores and usually only 4 or 5 ripe seeds are found on a single spike.

The development of the bract is initiated by the formation of a rounded lateral projection from just below the growing point of the axis (fig. 24). This protuberance soon begins to flatten at the end

and thus ultimately gives rise to the characteristic, short-stalked, orbicular bract. It has an epidermis sprinkled with oil cells and hydathodes, and within is a short, simple branch from the vascular bundle of the axis (figs. 25, 56). This bract reaches essentially its mature size, $125\ \mu$ in diameter, before the embryo sac of the same flower is ripe (figs. 22, 56, 78). As the fruit matures the bract shrivels somewhat but remains attached to the axis, even after the fruit has fallen. It is evident that this bract does not, except in the very earliest stages of the flower, protect the latter from desiccation or other injury (figs. 22, 56, 78). This subtending bract of the flower plays a far more important part in shielding the young flower in the cases of the more xerophytic species of *Peperomia*, as we shall have occasion to point out in a later paper.

C. THE DEVELOPMENT OF THE STAMEN, MICROSPORE AND POLLEN TUBE.

The stamen of *Peperomia hispidula* arises by the outpushing of a group of 8 or 10 periblem cells on each side of the young floral bract, and below the carpel which is developing at the same time just above the bract (figs. 25, 26, 27). When the group of hypodermal cells at the end of the young stamen has reached the number of about 40 or 50, there appear, in two regions where the microsporangia are to be formed, numerous periclinal walls in these cells (figs. 29, 30). The inner of the two layers thus formed gives rise to the definitive archesporium or sporogenous layer of the microsporangium. The outer layer is a primary parietal layer, the cells of which soon divide by periclinal walls into two series. The outer series of cells thus formed constitutes the fibrous layer or endothecium of the mature anther wall. The inner of the two series divides once more by periclinal walls forming the single tapetal layer within and an outer layer, lying next the endothecium, which becomes the innermost layer of the wall of the mature anther (figs. 33, 34). In the mature microsporangium the epidermal cells have thin, uncutinized and collapsed outer walls. The endothecium of the mature anther is about $20\ \mu$ thick, and consists of polygonal cells, 20 to $25\ \mu$ in diameter, with thin outer walls and thick inner ones. The lateral walls have 15 or 20 rib-like thickenings, which are really radial projections of the basal or inner wall (fig. 34). The nuclei of these cells, like those of the epidermis, degenerate and flatten out as the anthers ripen. The cells of the layer next within the endo-

thecium are represented in the mature stamen only by nearly collapsed cells with degenerating nuclei. The cells of the tapetal layer itself are well-developed at the time the microspore mother-cells are mature, and have dense cytoplasts with large nuclei (fig. 32). With the maturing of the anther the cytoplasts become thin, and the nuclei follow those of the other layers in gradually degenerating.

The opening of the ripe anther is evidently accomplished chiefly by the change in form of the endothecial cells, though this process has not been studied minutely. The rupture of the anther walls occurs along the series of smaller cells at the juncture of the two microsporangia (fig. 34). In sections of the opened anther (fig. 22, above middle of spike) it is seen that the outer walls have bent in and in consequence the anther walls have become completely everted, and the inner surface strongly convex. Soon after the anther is emptied the filament breaks off, leaving only a short stump projecting from the base of the ovary (fig. 22).

From the definitive archesporium, just within the parietal layer, are developed, chiefly by periclinal divisions, the one hundred or more microspore mother-cells of each microsporangium (figs. 31, 32). The sporogenous cells increase in size from a diameter of 8 or 10 μ , when first cut off, to one of 12 to 18 μ at the time of synapsis in the spore mother-cell (figs. 29, 32). The nuclei in the meantime increase from 5 or 6 μ to 10 or 12 μ in diameter, and the bulk of the chromatin also increases slightly up to the time of synapsis. The nucleoli of the definitive archesporial cells are usually single, and do not vary greatly from 2 or 3 μ in diameter in the resting nucleus throughout the development.

It will be well to emphasize at this point the fact that though the number of sporogenous cells in each sporangium varies, as was suggested in the last paragraph, no cases were seen in which the number of microsporangia was greater or less than two. There is thus no evidence from the development that this stamen ever had more than two microsporangia, and no examples were seen of the marked variability in the number of degrees of development of these that occurs in *Piper betel* (see Johnson, 1910). The only suggestions of this are found in those rare cases where the terminal flower of a spike may be pistillate only, and in the fact that from 10 per cent to 25 per cent of the nearly matured microspores in a stamen may prove sterile (fig. 34). The latter condition is not unusual among angiosperms as

a whole and therefore is of no special significance in this case. It is surprising that in all of the *Peperomias* thus far studied there is no indication of the derivation of the bisporangiate stamen of this genus from the four-sporangiate stamen possessed by other genera of the Piperaceae, in common with the great bulk of other angiosperms. This loss of all traces of a four-sporangiate phase of the stamen, through which it seems evident that it must have passed in its phylogeny, is an important fact. It will be well for us to have this fact in mind, when later we note the lack of any clear traces in the ontogeny of the phylogenetic origin of the peculiar type of embryo sac found in this genus.

The nuclear phenomena occurring during the division of the sporogenous cells, and during the maturing of the spore-mother cell and its division into the spores, are essentially typical. The appearance of the chromatin net and nucleolus of the resting nuclei, formed during this development, remain practically constant up to the time of preparation for synapsis in the nucleus of the spore mother-cell. During the earlier divisions of the archesporial cells and their nuclei, divisions may not occur at the same time in the different cells (fig. 29). As the time for synapsis approaches, however, the nuclear changes go on at very nearly the same rate in all the mother cells of the same sporangium (fig. 32). The nuclear phases may differ slightly in rate of progress in the two sporangia of the same stamen. The chromatin net of the mother-cell, just before synapsis, is rather large-meshed in parts, and is roughened with many granules (fig. 36). The first evidences of the approach of synapsis are a loosening up of the net and an increase in size, apparently accompanied by a decrease in number, of the chromatin grains, until these become nearly as large and of very closely the same number as the chromosomes of the sporophyte (fig. 37). At this early phase of synapsis the chromatin framework is still distributed about the whole periphery of the nuclear cavity, most of it lying close to the wall. The nuclei of the stamen in the same spike, next older than the stamen whose nuclei show the arrangement just described, have each a tangled chromatin thread that is distinctly contracted away from the nuclear wall. In such a nucleus but few chromatin granules are visible. The completely contracted synaptic knot stage follows very soon after the stage just mentioned, and in it the nucleolus and all of the chromatin, except a few outlying granules are compacted into a rounded mass occupying less than a

tenth of the nuclear cavity (figs. 38, 39). As the nucleus emerges from synapsis some of the constituent chromatin threads are loosened up, thus again becoming visible. Some portions of the thread are distinctly beaded (fig. 40). This loosening up of the chromatin thread continues till, from the synaptic knot, a slender, beaded, loosely coiled spireme is formed, which lies chiefly near the periphery of the nuclear cavity. Some loops of this spireme are evidently double (fig. 41). From this time onward the spireme thickens, and where the beading is at all distinct, the chromatin masses are evidently larger. Figure 41, for example, is of a nucleus the thick spireme of which is evidently just about to segment into chromosomes. In the other sporangium of the anther from which the latter figure was drawn the mother-cell nuclei had already divided.

There is nothing peculiar about the spindle formed in the two divisions of the nucleus of the microspore mother-cell. The chromosomes of the first division are about $1\ \mu$ thick and 2 or $3\ \mu$ long, and are bent to U-shaped or V-shaped bodies so that it is difficult to count them with certainty (figs. 42, 43). The character of the chromosomes before and during this division was not made out in sufficient detail to demonstrate the occurrence of a true reducing division here. The two chromosome groups resulting from this first division become organized into definite nuclei, with a distinct nuclear wall and a coarse peripheral net of chromatin. In the latter there can often be distinguished about 14 larger chromatin grains or masses which range from a half μ to one μ in thickness (fig. 44). Remains of the first spindle are clearly seen even at this stage. The chromosomes formed at the second division are 12 or 14 in number, and are at first much more rounded than those of the first division. Even when they move toward the poles these chromosomes are but slightly elongated and not much bent. The spindle of this second division persists, and by it, together with the remains of the spindle of the first division, the four spore nuclei, when first formed, are connected together (fig. 45).

The microspores of the tetrad are cut out in the usual manner, and the nucleus of each shows then a well-developed, fine-meshed chromatin net (figs. 46, 47). By the time the tetrahedral spore has rounded out to a globular form, and before the exine has become much thickened, the nucleus of the pollen grain divides to two (figs. 48, 49). One of these two nuclei soon becomes twice the bulk of the other (fig. 50). The larger, probably the pollen tube nucleus, lies nearer the wall of

the pollen grain. The cytoplasm about the smaller, more centrally placed, generative nucleus becomes denser and less vacuolated than the peripheral cytoplasm. Then a spherical mass of the latter, about half the diameter of the pollen grain, is cut off from the rest of the cytoplasm by a spherical cleavage surface or wall (fig. 50). The exact method of formation of this cleavage wall was not made out. Neither could a definite cellulose wall be demonstrated. In some spores, however, a considerable shrinkage space could be seen between the dense central and the vacuolated peripheral cytoplasm. This central, spherical mass may come into contact with the inner wall of the microspore, but never seems to become appreciably flattened against it, as often happens in the microspores of other angiosperms. This line of separation between the generative cell and the rest of the microspore is still visible in the ripe pollen grain (fig. 51). The nucleus of the generative cell has by this time become equal in size to the pollen tube nucleus. The brownish exine of the ripe pollen grain is greatly roughened by rounded wart-like protrusions, while the intine remains colorless, smooth and about three times the thickness of the exine (figs. 50, 51).

The germination of the pollen grain on the stigma and the fate of the two nuclei mentioned have not been observed. Structures have been seen in the interior of the style that stain differently than the surrounding tissue, and look like pollen tubes, but in no case could anything be made out of the contents of these tubular structures, and their identity as pollen tubes is not absolutely established.

The above account of the development of the stamens and ripe microspores has been given in some detail for the sake of making it evident that there are no clearly primitive features in this phase of the development of this, in many respects, simplest of the *Peperomias*. Some details of the history of the chromatin of the spore nuclei have been given because the sequence of stages can be followed with such certainty in the successive flowers of the spike. It will also be important for us to have these details in mind when discussing the origin of the embryo-sac nucleus, where the occurrence of a typical reduction division is of critical value in interpreting the nature of the mature embryo-sac.

EXPLANATION OF PLATES XXXVI-XXXVIII

All figures are camera drawings and are from hand sections or microtome sections, except figures 1, 2, 18 and 22.

The magnification given in the description of each figure is that actually shown by the figure as printed on the plate.

Abbreviations used: *A*, air chamber; *As*, archesporium; *Ax*, axis; *Br*, floral bract; *Bs*, bristle of fruit; *C*, carpel; *Cp*, chloroplast; *D*, nuclear disc; *DAs*, definitive archesporium; *E*, egg; *Ed*, endosperm; *EdN*, endosperm nucleus; *Em*, embryo; *En*, endodermis; *F*, fungus hyphae; *FL*, fore-leaf; *H*, hydathode; *In*, integument; *L*, leaf; *Mp*, micropyle; *Nc*, nucellus; *No*, nucleolus; *Oc*, oil-containing cell; *Osp*, oospore; *P*, perisperm; *Pa*, parietal layer; *PG*, pollen-grain; *Pl*, phloem; *PMC*, pollen mother-cell; *PPa*, primary parietal layer; *Pr*, peripheral cell; *S*, stem, *SF*, spindle fibers; *Sg*, stigma; *Sp*, spike; *St*, stamen; *Sy*, synergid; *Tp*, tapetum; *Tr*, trichome; *VB*, vascular bundle; *W*, wing of stem or decurrent margin of petiole.

FIG. 1. Surface view (glycerine mount) of terminal portion of mature plant, showing stem, two spikes and the position and structure of leaves. $\times 2\frac{1}{2}$.

FIG. 2. Optical section (glycerine mount) of trichome on stem opposite base of leaf. $\times 117$.

FIG. 3. Part of vertical section of leaf, with multicellular trichome. $\times 117$.

FIG. 4. Longitudinal section of tip of primary root. $\times 117$.

FIG. 5. Part of longitudinal section of mature root, showing vascular bundle, crinkled endodermis and cortex. $\times 216$.

FIG. 6. Transverse section of mature root, showing vascular bundle, endodermis, root hairs, and fungus hyphae in cortex. $\times 117$.

FIG. 7. Part of radial section of root, showing penetration of cell walls of cortex by fungus hyphae. $\times 216$.

FIG. 8. Portion of similar section, showing a much swollen hypha. $\times 216$.

FIG. 9. Part of tangential section of root showing crinkled radial walls of endodermis. $\times 216$.

FIG. 10. Transverse section of stem. $\times 28$.

FIG. 11. Transverse section of stele of stem. $\times 117$.

FIG. 12. Part of longitudinal section of young stem (peduncle), showing epidermis with oil cells and hydathodes. $\times 400$.

FIG. 13. Part of longitudinal section of mature stem, showing structure of cell wall of epidermis. $\times 340$.

FIG. 14. Transverse section of petiole. $\times 36$.

FIG. 15. Transverse section of median vascular bundle of petiole. $\times 252$.

FIG. 16. Part of transverse section of leaf including its midrib (glycerine mount). $\times 117$.

FIG. 17. Part of transverse section of leaf at margin (glycerine mount). $\times 117$.

FIG. 18. Part of lower surface of leaf, showing distribution of stomata, hydathodes and oil-cells, overlying water glands at apex of leaf (glycerine mount). $\times 117$.

FIG. 19. Surface view of typical stoma and its surrounding cells. $\times 216$.

FIG. 20. Transverse section of guard cells with cutinized margins (glycerine mount). $\times 400$.

FIG. 21. Longitudinal section of tip of leaf through gland at end of midrib. $\times 117$.

FIG. 22. Surface view of spike, showing young fruits and stamens with unopened and with empty anthers (glycerine mount). $\times 12$.

FIG. 23. Longitudinal section of fruit with terminal spike and two lateral axillary buds. $\times 27$.

FIG. 24. Longitudinal section of apex of a spike, showing growing point of stem and three floral bracts, in the axils of which carpels are being initiated, as indicated by the bulging and deeper staining of cells. $\times 166$.

FIG. 25. Longitudinal section of floral bract with young ovary. $\times 216$.

FIG. 26. Transverse section of base of bract through young ovary and stamens. $\times 216$.

FIG. 27. Transverse section of stamen of the age shown in last figure. $\times 405$.

FIG. 28. Transverse section of bract with half grown ovary and stamens. $\times 63$.

FIG. 29. Longitudinal section of young stamen. $\times 540$.

FIG. 30. Transverse section of slightly older stamen. $\times 540$.

FIG. 31. Transverse section of stamen showing three-layered wall, definitive tapetal layer, and young pollen mother-cells. $\times 315$.

FIG. 32. Transverse section of stamen with nuclei of pollen mother-cells in synapsis. $\times 315$.

FIG. 33. Longitudinal section of nearly mature stamen. $\times 148$.

FIG. 34. Transverse section of nearly mature stamen. $\times 148$.

FIG. 35. Transverse section of stele of axis of spike, midway its length. $\times 360$.

FIG. 36. Section of mature pollen mother-cell, just before the beginning of synapsis. $\times 1,300$.

FIG. 37. Section of pollen mother-cell at the beginning of synapsis. $\times 1,315$.

FIG. 38. Similar section showing later phase of synapsis. $\times 900$.

FIG. 39. Similar section showing complete synapsis. $\times 900$.

FIG. 40. Similar section showing beginning of recovery of nucleus of pollen mother cell from synapsis. $\times 1,315$.

FIG. 41. Similar section showing beginning of formation of chromosomes. Spireme double. $\times 1,315$.

FIG. 42. Similar section showing part of chromosomes in first division of pollen mother-cell. $\times 1,315$.

FIG. 43. Transverse section of spindle of first division of spore mother-cell, showing form of chromosomes in equatorial plate. $\times 1,315$.

FIG. 44. Section of pollen mother-cell showing the daughter nuclei organized after first division. $\times 1,125$.

FIG. 45. Similar section showing four pollen nuclei still connected by fibers. $\times 1,315$.

FIG. 46. Similar section showing tetrad of young pollen grains. $\times 900$.

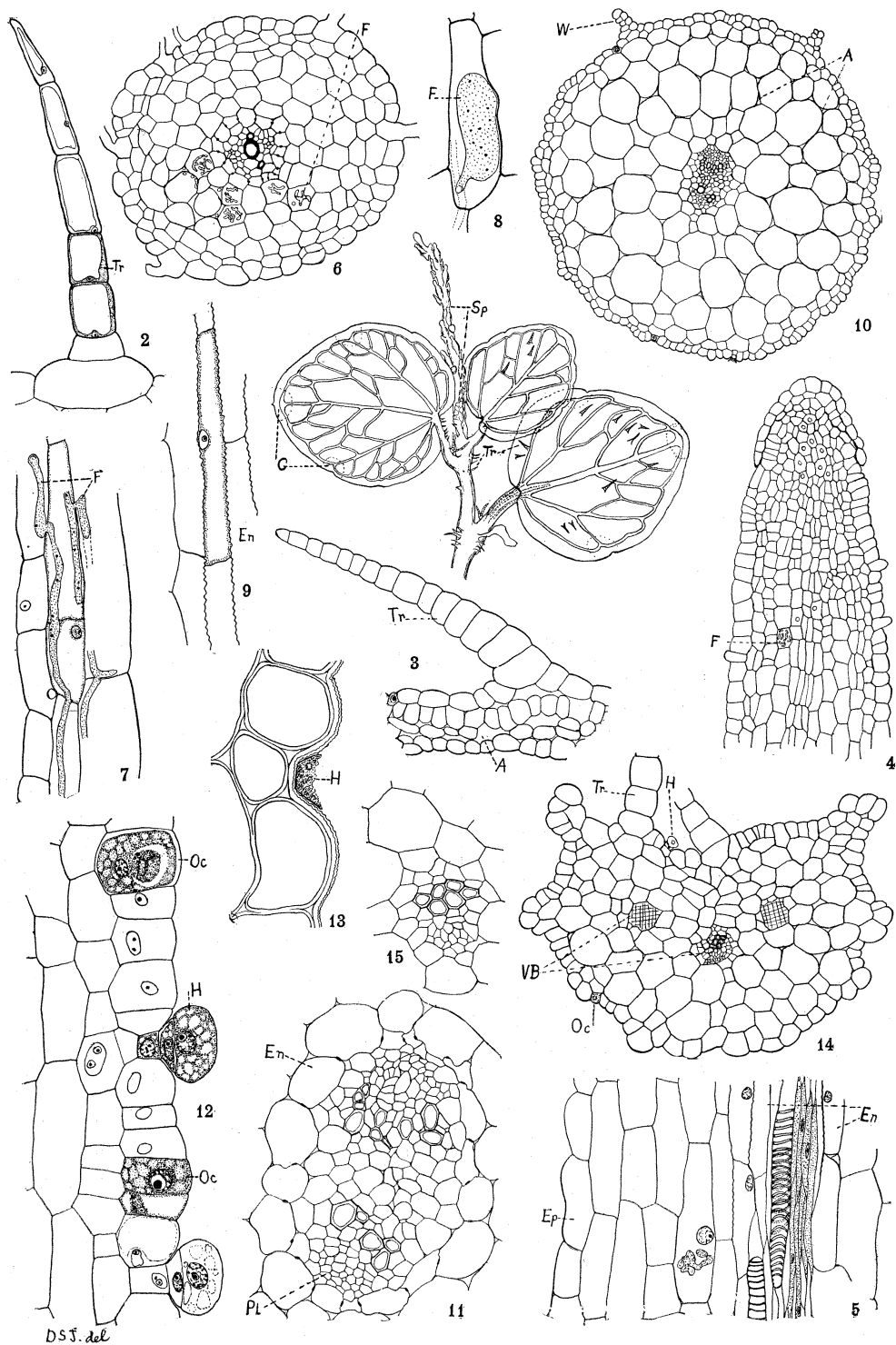
FIG. 47. Section of uninucleate pollen grain, with large central vacuole and partly thickened wall. $\times 1,315$.

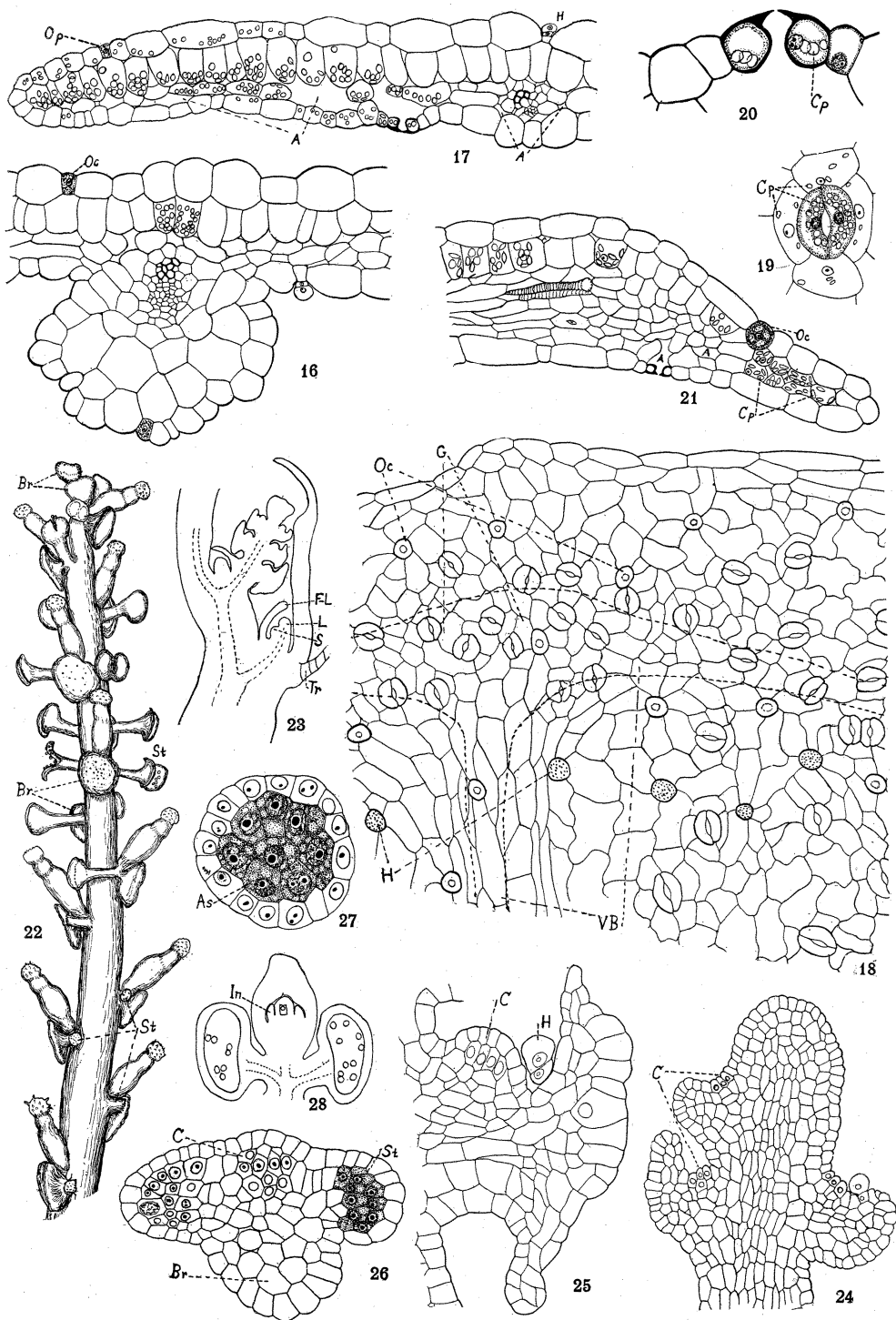
FIG. 48. Section of older pollen grain showing numerous small vacuoles. $\times 1,315$.

FIG. 49. Section of pollen grain with spindle for division into pollen tube nucleus and generative nucleus. $\times 1,315$.

FIG. 50. Section of pollen grain showing generative nucleus with some cytoplasm cut off by cell wall. $\times 1,315$.

FIG. 51. Section of mature pollen grain still showing faintly the outline of the generative cell. $\times 1,315$.





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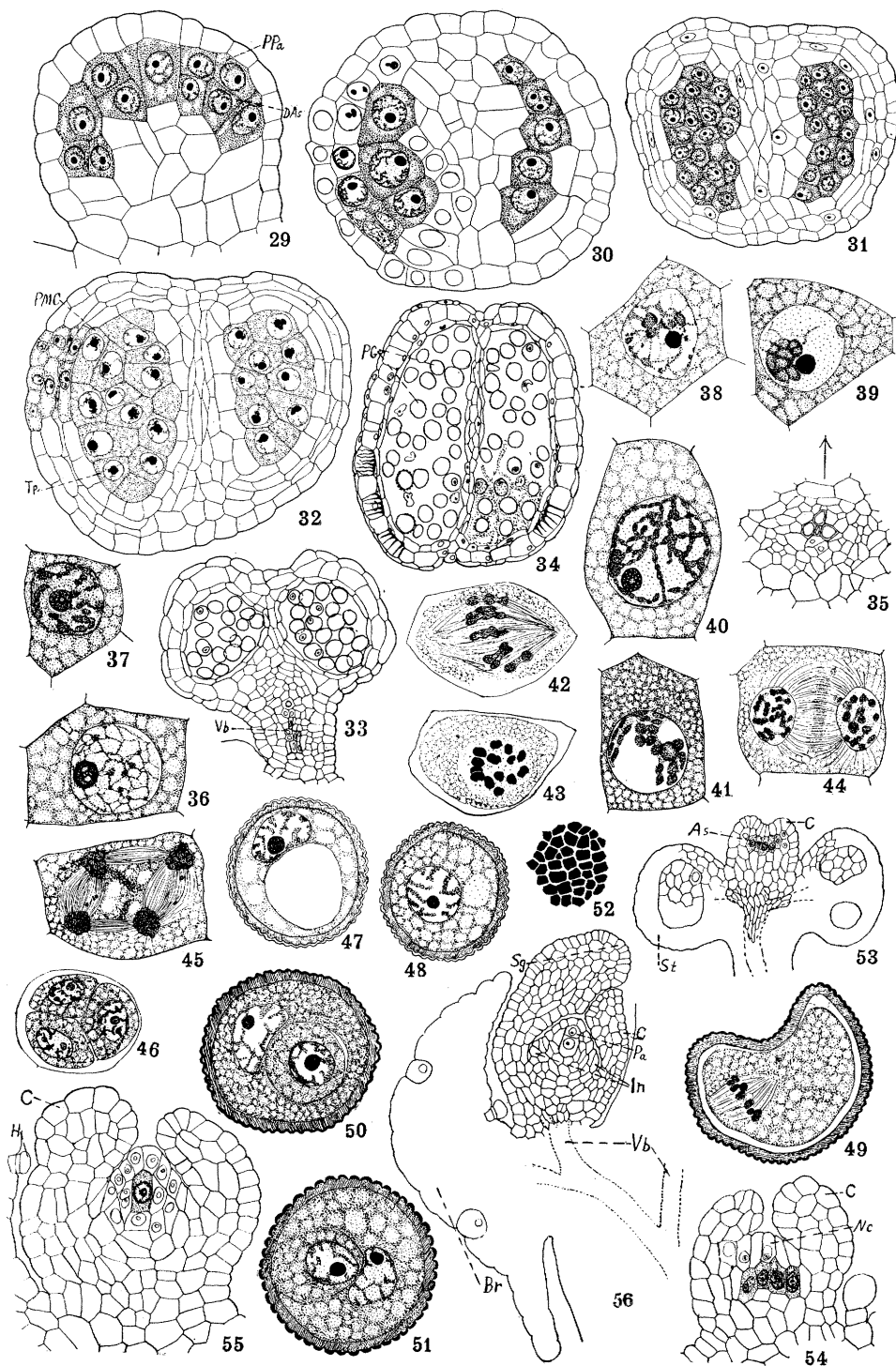


FIG. 52. Section showing surface of wall of mature pollen grain. $\times 1,315$.

FIG. 53. Approximately longitudinal section through young flower, showing ovule and two stamens. $\times 148$.

FIG. 54. Longitudinal section of young ovary. $\times 148$.

FIG. 55. Longitudinal section of ovary, showing carpels and primary archesporial cell of ovule. $\times 338$.

FIG. 56. Longitudinal section of ovary and subtending bract, showing vascular connection of these with floral axis. Definitive archesporial cell and parietal cell in ovule. $\times 148$.